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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *PAROXYNA GENALIS* (THOMSON) (DIPTERA: TEPHRITIDAE) ON NATIVE ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Paroxyna genalis* (Thomson) is a multivoltine tephritid that develops in flower heads of a broad spectrum of Asteraceae in California. The egg, first through third-instar larvae, and puparium are described and figured for the first time. Distinctive morphological differences noted for these immature stages are in the sensilla comprising the lateral spiracular complexes of the meso- and metathorax and in the distribution and incidence of rugose pads on the anterior of the prothorax of the third instar larva. The larvae feed mainly on the ovules and soft achenes, but also may score the receptacle and imbibe sap at fresh wounds in these structures. Pupariation occurs in the larval feeding chamber among fragments of scored achenes. Premating and mating behaviors are described, including a characteristic, uplifted-wing movement newly designated as "lofting." Mate-guarding behavior by males following copulation is reported, apparently the first example among Holarctic Tephritidae. The principal natural enemies of immature *P. genalis* were the solitary, primary, larval-pupal, endoparasitic, chalcidoid Hymenoptera, *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae).

Key Words: Insecta, *Paroxyna genalis*, nonfrugivorous Tephritidae, mating behavior, immature stages, Asteraceae, flower-head feeding

Twenty-one species of *Paroxyna* are known from North America north of Mexico (Novak 1974, Foote et al. 1993), but only the life history and immature stages of *P. albiceps* (Loew), a common species in the northeastern United States, have been described in detail (Novak and Foote 1968). This paper describes the life history and immature stages of a second Nearctic species, *P. genalis* (Thomson), the most commonly encountered *Paroxyna* in California (Goeden 1994) and an adopted natural enemy of the alien weed, tansy ragwort, *Senecio jacobaea* L. (Frick 1964).

MATERIALS AND METHODS

Locating field populations of *P. genalis* reasonably accessible from Riverside allowed us to complete this study principally on *Eriophyllum lanatum* (Thomson) and *Senecio mohavensis* Gray, two of its many recently reported host plants (Goeden 1994). Field observations primarily were made on *E. lanatum* at a study site located in a gently sloping, dry clearing among conifers at 2030-m elevation in the National Children's Forest, San Bernardino National Forest (northern section), San Bernardino Co., during 1990–92. Flower heads containing eggs, larvae, and puparia were sampled at this and additional locations on this and other host-plant species reported below and elsewhere (Goeden 1994). *Senecio mohavensis* was sampled weekly during February and March, 1993, at 260-m elevation in Box Canyon, Riverside Co., in the Col-

orado Desert. One-liter samples of flower heads were returned to the laboratory for dissection, photography, description, and measurement, or for bulk cagings in glass-topped sleeve cages in the insectary of the Department of Entomology, University of California, Riverside, at 27 ± 1°C and a 14-h photoperiod (Goeden 1985, 1989). All eggs, larvae, and 12 puparia dissected from these heads were preserved in 70% EtOH for scanning electron microscopy (SEM). All other puparia were placed in separate glass rearing vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult emergence. Specimens for SEM later were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia, as well as overwintered adults swept from preblossom and early blossom *E. lanatum*, were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests. Virgin male and female flies obtained from emergence vials, as well as field-collected adults, were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey for direct observations, videorecording, and still-photography of their general behavior, courtship, and copulation (Headrick and Goeden 1991). Six pairs were held together for at least 14 d and observations were made as opportunity allowed throughout each day.

Plant names used in this paper follow Munz and Keck (1959) and Munz (1968, 1974); names for flower-head parts follow Hickman (1993). Tephritid names and anatomical terms follow Foote et al. (1993); nomenclature used to describe the immature stages follows Headrick and Goeden (1990, 1991), Goeden and Headrick (1990, 1991a, b, 1992), and the telegraphic format of Goeden et al. (1993). Means ± SE are used throughout this paper. Voucher specimens of reared adults of *P. genalis* and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in separate collections of immature Tephritidae maintained by DHH and JAT.

Results and Discussion

Taxonomy

Thomson (1869) first described *P. genalis* (as a *Trypeta*), and this variable species since has acquired several synonyms (Foote et al. 1993). Foote and Blanc (1963) pictured the wing of *P. genalis* [also under the synonyms, *americana* Hering and *corpulenta* (Cresson)], and Novak (1974) described and illustrated the wing, male genitalia, ejaculatory apodeme, and aedeagus (also as *americana* and *corpulenta*). The immature stages have neither been described nor illustrated.

Egg.—Egg body smooth, shiny, white, elongate-ellipsoidal; ovum covered by a smooth, membranous sheath (Fig. 1A); anterior end blunt bearing nipple-like, 0.016 mm-long, 0.04 mm-wide pedicel (Fig. 1B); posterior end tapered. Seventeen eggs dissected from heads of *E. lanatum* averaged 0.64 ± 0.01 (range, 0.53–0.67) mm in length, 0.19 ± 0.003 (range, 0.17–0.21) mm in width (Figs. 1A, 6A); 23 eggs dissected from heads of *S. mohavensis* averaged 0.64 ± 0.01 (range, 0.56–0.72) mm in length, 0.19 ± 0.002 (range, 0.17–0.21) mm in width (Fig. 6B).

The eggs of *P. albiceps* described by Novak and Foote (1968) are similar in appearance, but most were longer and all were wider. The eggs also were similar in ap-

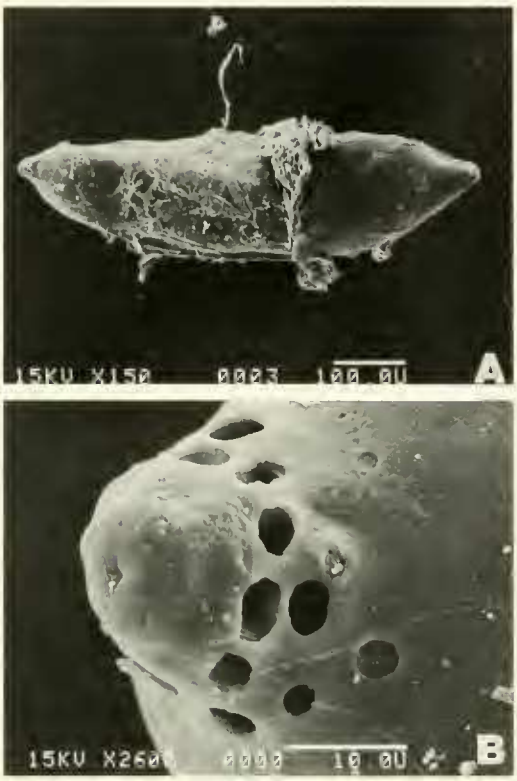

Fig. 1. Egg of *P. genalis*: (A) habitus, dissected from *E. lanatum*, anterior end at left; (B) detail of pedicel, showing aeropyles.

pearance to those of *Trupanea bisetosa* (Coquillett) (Cavender and Goeden 1982), *T. conjuncta* (Adams) (Goeden 1987), *T. imperfecta* (Coquillett) (Goeden 1988), *T. californica* Malloch (Headrick and Goeden 1991), and *T. nigricornis* (Coquillett) (Knio and Goeden, unpublished data). *Paroxyna genalis* eggs were similar in width, but shorter in length than all species except *T. californica*. Differences occurred in size and shape of the pedicel and the number of aeropyles. *Tephritis baccharis* (Coquillett) (Goeden and Headrick 1991b) and *T. arizonaensis* Quisenberry (Goeden et al. 1993), also in the Tribe Tephritini (Foote et al. 1993), differ dramatically in egg shape from *P. genalis* and the *Trupanea* spp. mentioned above.

Third instar.—Third instar superficially smooth, elongate-ellipsoidal, tapering anteriorly, truncated posteriorly; minute acanthae laterally and along intersegmental lines (Fig. 2A); gnathocephalon conical, with few rugose pads; pads laterad of mouth lumen serrated ventrally (Fig. 2B-1); paired dorsal sensory organs dorsad of anterior sensory lobes each consisting of a single, dome-shaped papilla (Fig. 2C-1); anterior sensory lobes bear the lateral sensory organ (Fig. 2C-2), pit sensory organ (Fig. 3C-3), terminal sensory organ (Fig. 2C-4), and an additional sensillum dorsad of the lateral sensory organ (Fig. 2C-5); stomal sense organs lie ventrad of anterior sensory lobes near mouth lumen (Fig. 2C-6); mouth hooks bidentate, teeth stout, bluntly conical (Fig. 2B-2); median oral lobe laterally flattened, attached to labial lobe; anterior thoracic spiracles located dorsolaterally on posterior margin of prothorax which bears four or five papillae (Fig. 2D); lateral spiracular complex on the mesothorax and metathorax composed of an open lateral spiracle (Fig. 2E-1), two verruciform sensilla (Fig. 2E-2), and a dorsal stelex sensillum (Fig. 2E-3); lateral spiracular complex on abdominal segments composed of an open lateral spiracle (Fig. 2F-1), three verruciform sensilla (Fig. 2F-2),

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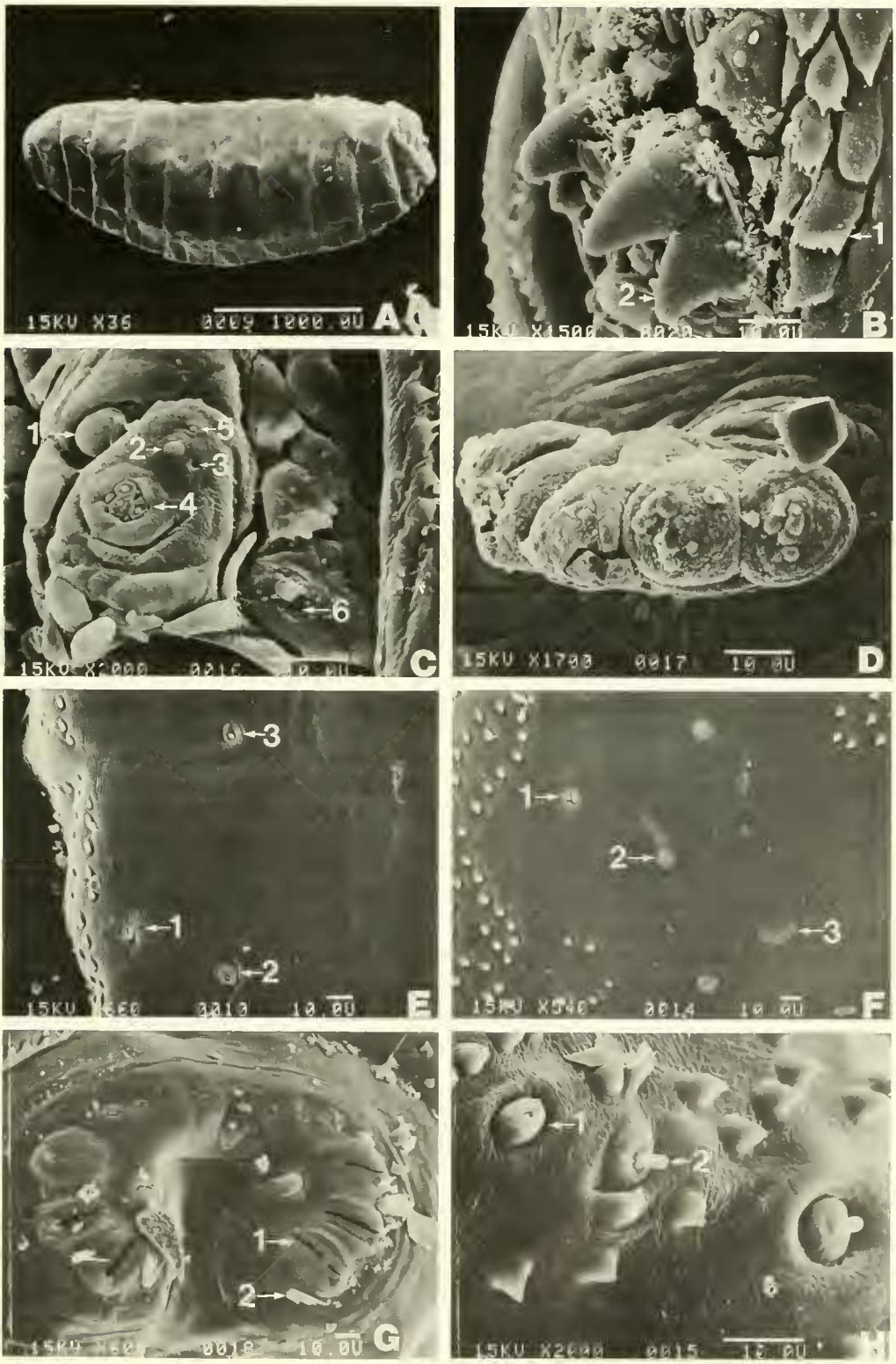
Fig. 2. Third instar larva of *P. genalis*: (A) habitus, anterior to left; (B) gnathocephalon, left lateral view, 1—serrated rugose pads, 2—mouth hooks; (C) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—terminal sensory organ, 5—unnamed sensillum, 6—stomal sense organ; (D) anterior thoracic spiracle; (E) lateral spiracular complex, metathorax, 1—spiracle, 2—verruciform sensilla, 3—stelex sensillum; (F) lateral spiracular complex, first abdominal segment, 1—spiracle, 2—verruciform sensilla, 3—campaniform sensillum; (G) caudal segment, 1—rima, 2—interspiracular process; (H) caudal segment, compound sensillum, 1—tuberculate, medusoid chemosensillum, 2—stelex sensillum.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and a larger, slightly raised, campaniform sensilla (Fig. 2F-3); caudal segment bears posterior spiracular plates (Fig. 2G); plates bear three elongate-oval rimae ca. 0.03 mm long (Fig. 2G-1), and four interspiracular processes with three to five branches each, the longest measuring 0.01 mm in length (Fig. 2G-2); stelex sensilla surround margin of caudal segment in four-dorsal, six-ventral arrangement; caudal segment additionally bears a pair of compound sensilla ventrad of the spiracular plates consisting of a tuberculate, medusoid, chemosensillum resting in a shallow depression (Fig. 2H-1) and a stelex sensillum (Fig. 2H-2).

The genus *Paroxyna* is closely related to *Trupanea* (Foote et al. 1993), but the third instar of *P. genalis* shows some differences from that of *T. californica* (Headrick and Goeden 1991). The gnathocephalon bears fewer rugose pads, and the sensory lobes are smaller than those of *T. californica*. The anterior margin of the prothorax is smooth in *P. genalis*, lacking the band of rugose pads observed in *T. californica* and other *Trupanea* species examined by us (unpublished data). The ventrally serrated, rugose pads located near the mouth lumen in *P. genalis* are similar to those of *T. bisetosa* and *T. nigricornis* (Knio and Goeden, unpublished data). The anterior thoracic spiracles are similar to those of *T. californica* (Headrick and Goeden 1991). The lateral spiracular complex of the meso- and metathorax in *P. genalis* differs from the abdominal segments in that the dorsal-most sensillum is a stelex sensillum instead of a verruciform sensillum. No other tephritid species examined by us to date have a stelex sensillum associated with its lateral thoracic spiracle. The compound sensilla ventrad of the posterior spiracular plates in *P. genalis* are similar to those illustrated for *Tephritis arizonaensis* (Goeden et al. 1993), *Trupanea bisetosa*, and *Trupanea nigricornis* (Knio and Goeden, unpublished data).

Second instar.—Second instar superficially smooth, elongate, cylindrical; minute acanthae circumscribing larva along the intersegmental lines (Fig. 3A); gnathocephalon conical, dorsally and laterally flattened, smooth, no rugose pads laterad of the mouth lumen; few petals dorsad of the mouth lumen (Fig. 3B-1); paired dorsal sensory organs dome-shaped, dorsomedial to the anterior sensory lobes (Fig. 3B-2, 3C-1); anterior sensory lobes flattened, small, bearing a lateral sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), terminal sensory organ (Fig. 3C-4), and an additional sensillum dorsad of the lateral sensory organ (Fig. 3C-5); stomal sense organs located ventrad of the anterior sensory lobes, near the lateral aspect of the mouth lumen (Fig. 3B-3); mouth hooks bidentate, teeth conical (Fig. 3B-4); median oral lobe laterally flattened, rounded ventrally, attached to floor of mouth lumen (Fig. 3B-5); anterior thoracic spiracles with four, rounded papillae (Fig. 3D); lateral spiracular complex on abdominal segments with three visible verruciform sensilla, however, the spiracle itself was obscured (Fig. 3E); caudal segment bears the spiracular plates; plates bear three oval rimae ca. 0.03 mm long (Fig. 3F-1) and four interspiracular processes, with three to five branches each, longest measuring 0.01 mm in length (Fig. 3F-2); stelex sensilla surround margin of caudal segment (Fig. 3F-3).

The second instar larva differs from the third instar in size and in that it is more cylindrical. The gnathocephalon lacks the serrated rugose pads near the mouth lumen, and the dorsal margin of the mouth lumen contains few integumental petals. In the second instar, the anterior sensory lobes are smaller and not as distinct, and the median oral lobe is distinctly laterally flattened. The lateral spiracular complex typically is not visible in second instars and has not previously been illustrated for any other tephritid species. This may be due in part to substantial morphogenesis of the spiracular system between instars as noted by Headrick and Goeden (1990) for *Paracantha gen-*

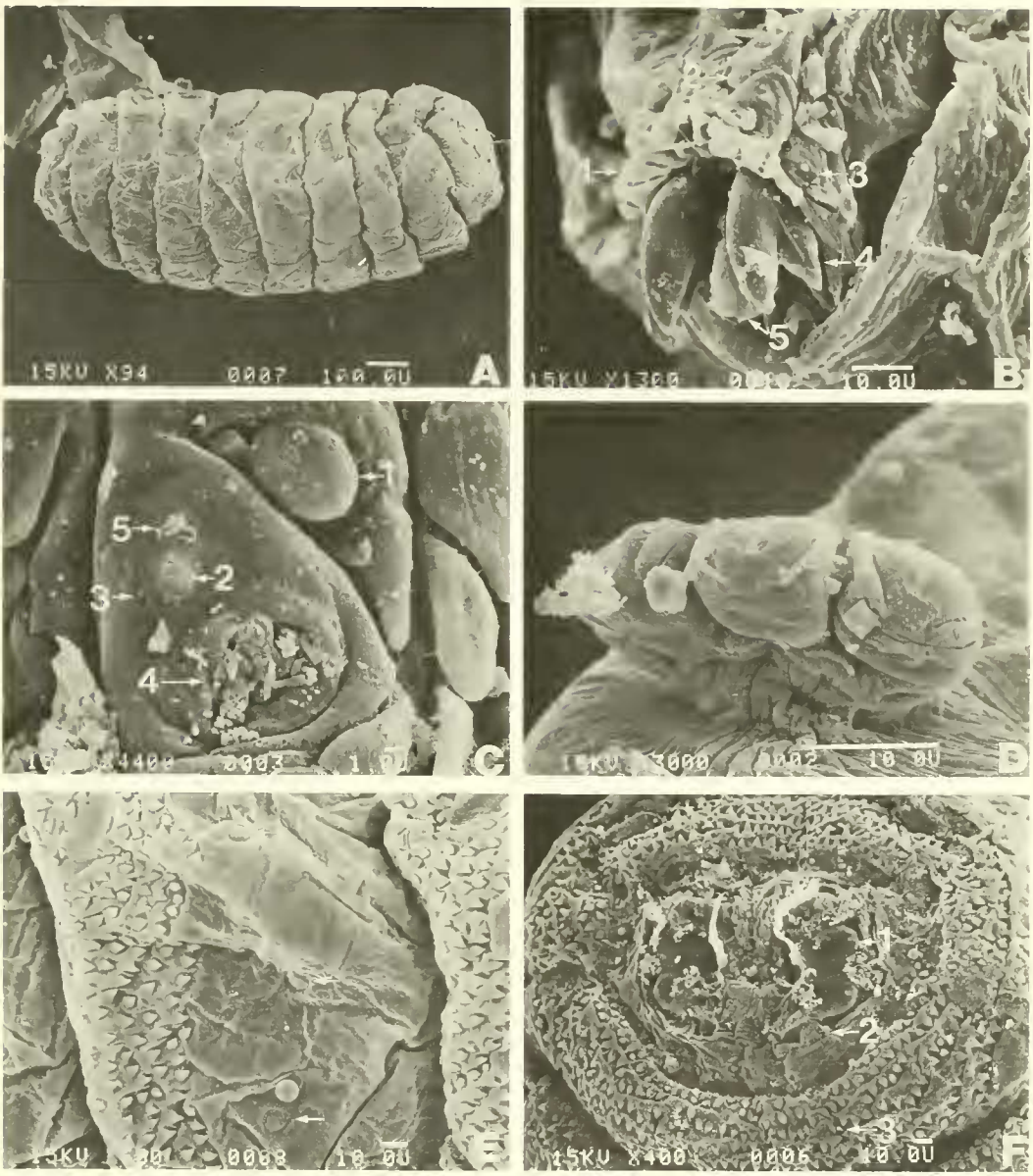

Fig. 3. Second instar larva of *P. genalis*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1—integumental petals, 2—dorsal sensory organ, 3—stomal sensory organ, 4—mouth hooks, 5—median oral lobe; (C) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—terminal sensory organ, 5—unnamed sensillum; (D) anterior thoracic spiracle; (E) lateral spiracular complex, abdominal segment, verruciform sensilla; (F) caudal segment, 1—rima, 2—interspiracular process, 3—stelex sensillum.

tilis, and because all of our larval specimens were dissected from plant samples and are not as free of debris and lipid residues as laboratory reared specimens.

First instar.—First instar cylindrical, tapered anteriorly, rounded posteriorly; gnathocephalon slightly conical, smooth, lacking petals or rugose pads (Fig. 4A); an-

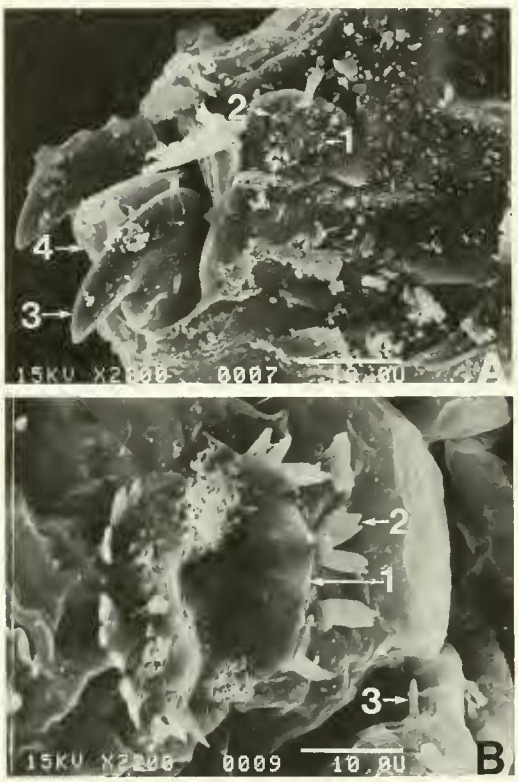

Fig. 4. First instar larva of *P. genalis*: (A) gnathocephalon, left lateral view, 1—lateral sensory organ, 2—terminal sensory organ, 3—mouth hooks, 4—median oral lobe; (B) caudal segment, 1—rima, 2—interspiracular process, 3—stelex sensillum.

terior sensory lobes flattened, bearing a lateral sensory organ (Fig. 4A-1) and a terminal sensory organ (Fig. 4A-2); mouth hooks bidentate, teeth thinly tapered (Fig. 4A-3); median oral lobe laterally flattened, rounded ventrally (Fig. 4A-4); anterior thoracic spiracles absent; lateral spiracular complex not observed; caudal segment lacking minute acanthae; posterior spiracular plates each bear two, oval rimae (Fig. 4B-1) and four, interspiracular processes with broad, apically serrate branches, longest branch measuring 0.005 mm in length (Fig. 4B-2); stelex sensillum seen ventrad of posterior spiracular plates (Fig. 4B-3).

The first instar larva differs from third instar in its size and general habitus, being more cylindrical. The sensilla of the anterior sensory lobes are small and indistinct with only the lateral and terminal sensory organs visible. Again, considerable morphogenesis takes place in sensory structures between subsequent instars in this and other species (Headrick and Goeden 1990). No lateral spiracles were observed, but they are present in first instars of *Trupanea bisetosa* and *Trupanea nigricornis* (Knio and Goeden, unpublished data); thus, further observations need to be made for this and other tephritid species to substantiate the presence of lateral spiracles in all three instars.

Puparium.—Puparium light to dark brown, elongate-ellipsoidal, rounded at both ends, superficially smooth, with minute acanthae laterally and along intersegmental lines (Fig. 5A); 87 puparia averaged 2.90 ± 0.03 (range, 2.00–3.53) mm in length, 1.30 ± 0.02 (range, 0.86–1.56) mm in width; anterior end bears invagination scar (Fig. 5B-1); raised anterior thoracic spiracles dorsolaterad of the invagination scar (Fig. 5B-2); posterior spiracular plates bear slightly raised, elongate-oval rimae, ca. 0.04 mm in length (Fig. 5C-1), and four, interspiracular processes with three to six branches, the longest measuring 0.02 mm in length (Fig. 5C-2); compound sensilla ventrad of the spiracular plates were retained (Fig. 5D).

Distribution and hosts

Novak (1974) recorded the distribution of *P. genalis* as California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington and Wyoming, and Alberta, British Columbia, and Saskatchewan in Canada. Its distribution in North America north of Mexico was mapped by Foote et al. (1993), who noted that this species possibly extends into Mexico.

Goeden (1994) analyzed the known host ranges of nine of the 19 species of *Paroxyna* from California and noted that *P. genalis* appears to be the sole generalist, i.e. attacking more than one tribe of Asteraceae, among them. *Paroxyna genalis* is now

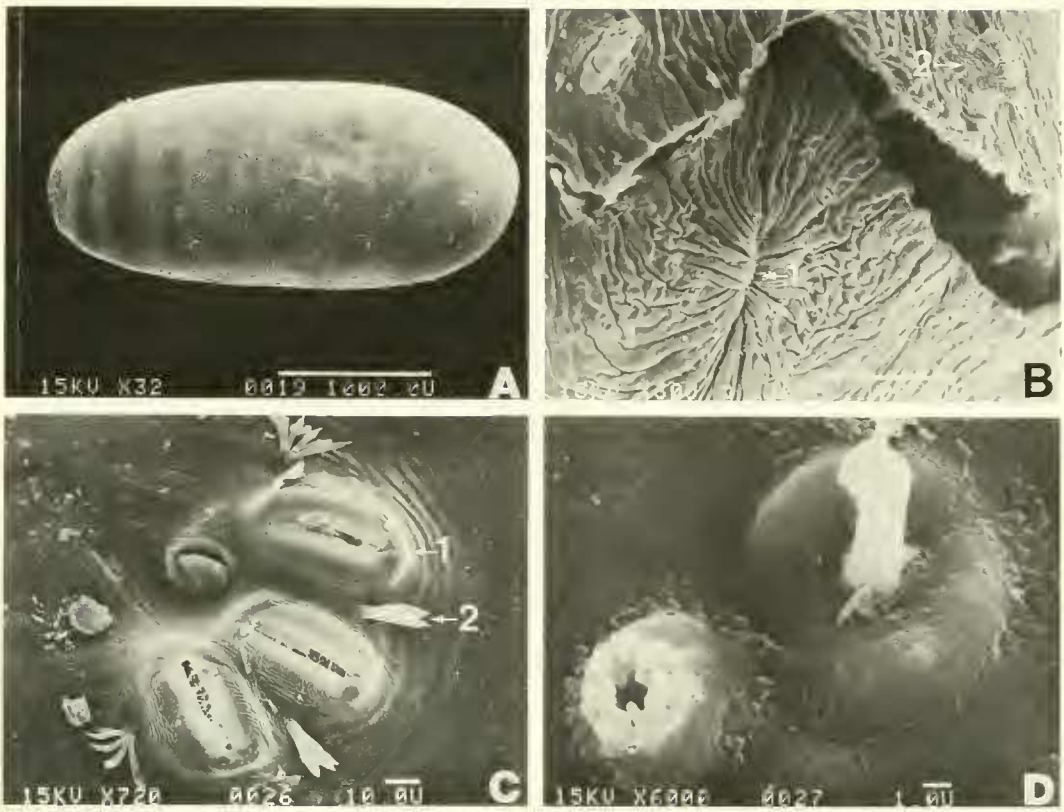

Fig. 5. Puparium of *P. genalis*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, posterior spiracular plate, 1—rima, 2—interspiracular process; (D) caudal segment, compound sensillum.

known from 16 genera and 38 species in six tribes: Astereae, Chicorieae, Helenieae, Heliantheae, Inuleae, and Seconioneae. Frick (1964) reared this native tephritid from flower heads of tansy ragwort in California, an accidentally introduced, range weed native to Europe and toxic to livestock, to which it had transferred, probably from one or more, native species of *Senecio*. This represents one of the few, documented, successful host-plant transfers of a native, nonfrugivorous tephritid to an alien Asteraceae (Goeden 1994).

Biology

Egg.—Eggs of *P. genalis* are inserted, pedicel-last, singly or side-by-side in pairs, and up to half their lengths, into the closed corolla or ovule of an immature floret in preblossom flower heads. Their long axes were oriented from between $<30°$ to perpendicular with the long axis of a head (Fig. 6A). Thirty, infested, field-collected heads of *Eriophyllum lanatum* contained from one to eight eggs or empty chorions and newly-eclosed first instars (suggesting oviposition by different females at different times in single heads), for an average of 4.0 ± 0.4 eggs per head. Most eggs were isolated and inserted into the florets around the periphery of a head, the ovipositor(s) having pierced the tightly overlapping phyllaries to reach them.

In closed, immature flower heads of *Senecio moharensis*, the eggs also were inserted into corollas or ovules for up to two-thirds

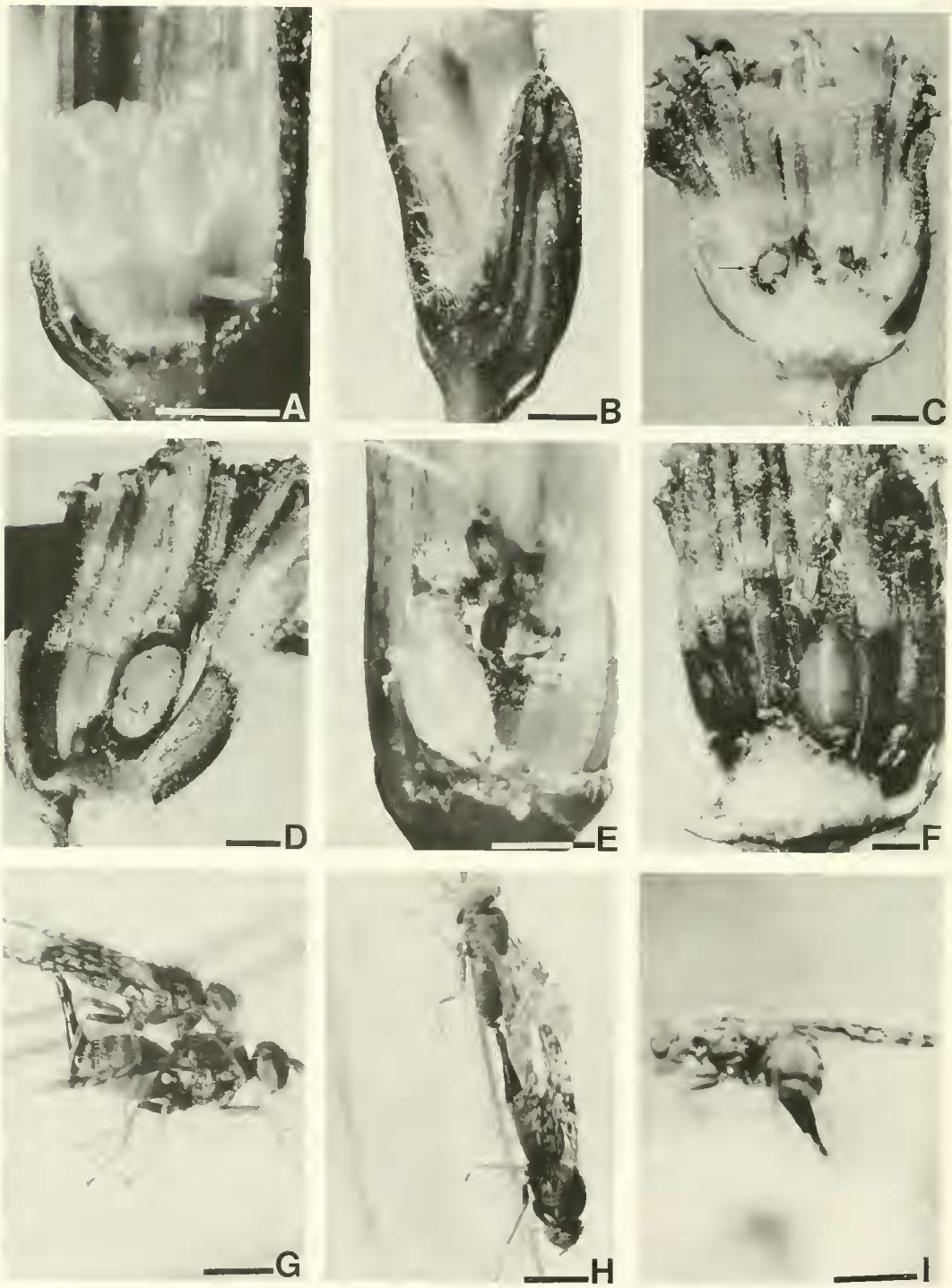

Fig. 6. Life stages of *P. genalis*: (A) egg inserted laterally in flower head of *Senecio mohavensis*; (B) swollen, infested head of *S. mohavensis*; (C) tunneling in soft achenes by two young larvae in head of *Eriophyllum lanatum*; (D) third instar in head of *E. lanatum*; (E) third instar in head of *S. mohavensis*; (F) puparium in head

their lengths as the ovipositor penetrated the phyllaries and damaged as many as five ovules in its passage. In one case, the aculeus of a female passed completely through two ovules with the egg deposited in a third. Twenty-five field-collected flower heads of *S. mohavensis* contained from one to three, and an average of 1.2 ± 0.1 eggs per head. At room temperature, the eggs hatched in about 4 days. Oviposition caused the receptacles of some heads to swell locally and the bracts to split apart over the oviposition wound, as a result of callous tissue formed around the egg (Fig. 6B).

In contrast, according to Novak and Foote (1968), the eggs of *P. albiceps* are laid pedicel-first, facing the receptacle near the centers of heads of *Aster* spp., and the ovipositor does not pierce the phyllaries; however, some eggs of *P. albiceps* similarly penetrate the disk florets; whereas, others are inserted between these florets. Accordingly, no tissue proliferation in response to oviposition by this tephritid was reported. Also, *P. albiceps* laid from one to five eggs per head.

Larva.—In *E. lanatum*, the newly hatched larva of *P. genalis* tunneled into the floral tube and down into the ovule, then this and the next instar bored cleanly through a succession of ovules and soft achenes leaving a narrow open tunnel as the heads concurrently opened, grew, and the achenes developed (Fig. 6C). The third instar confined its feeding to, and nearly consumed, three to six full-size, soft achenes, and also usually scarified the receptacle (Fig. 6D). The circular feeding scars in receptacles in heads of *E. lanatum* measured 1.02 ± 0.05 (range, 0.54–1.72) mm by 1.01 ± 0.04 (range, 0.60–0.172) mm in cross-diameter by 0.47 ± 0.05 (range, 0.21–1.72) mm deep (n = 37). Receptacle scarification was common, but not universal, as 32 (80%) of 40 third instars scored the receptacles in a sample of 50 infested, postblossom heads. Third instars presumably fed on sap that collected in these feeding scars, like certain other, nongallicolous, flower-head feeding Tephritidae, e.g. Headrick and Goeden (1990, 1991), Goeden and Headrick (1992), Goeden et al. (1993, 1994).

In *S. mohavensis*, first instars damaged an average of 3.0 ± 0.7 (range, 1–8) ovules (n = 9), second instars destroyed a cumulative average of 5.3 ± 0.5 (range, 1–11) ovules or soft achenes (n = 22), and heads with third instars (Fig. 6E) contained an average total of 14.9 ± 0.6 (range, 6–30) damaged ovules and soft achenes (n = 68). As 119 heads contained an average of 20.8 ± 0.4 (range, 13–30) achenes, and 27 heads each with a single puparium contained 16.2 ± 0.6 (range, 10–24) damaged achenes, seed destruction per head approximated 80%.

The total number of achenes damaged by *P. genalis* larvae in heads of *E. lanatum* averaged 12.6 ± 0.8 (range, 3–31) in 69 heads infested by single larvae, 23.4 ± 1.8 (range, 12–35) in 14 heads each infested by two larvae, and 33.7 ± 7.5 (range, 15–50) in four heads each infested by four larvae. A single head infested by five larvae contained 50 damaged achenes. As 87 infested heads contained an average total of 90 ± 2 (range, 45–138) achenes, for heads infested by one, two, or four larvae each, this represented average seed destruction rates per head of about 14%, 26%, and 37%, respectively. Fifty (37%) of a subsample of 136 heads, 30 (33%) of 90 heads, 30 (38%) of 79 heads, and 30 (46%) of 65 heads of *E. lanatum* collected in subsequent years and at other locations also were infested by *P. genalis*, demonstrating again that this te-

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of *E. lanatum*; (G) mating pair; (H) pair at termination of mating; (I) flower head viewed from above while female ovipositing laterally in closed, young flower head of *E. lanatum*.

phritid attacks only a portion of the flower heads and damages only a small part of the achenes produced by this host-plant species. Similarly, 20 (10%) of a subsample of 200 heads of *Crepis acuminata* Nuttall were infested by *P. genalis*. These 200 heads contained an average of 9.3 ± 0.6 (range, 5–15) achenes, 1.9 ± 0.2 (range, 1–4) of which (20%) were damaged by larval feeding. Furthermore, 30 (49%) of a subsample of 61 heads of *C. occidentalis* Nuttall were infested, and these heads contained an average of 10.5 ± 0.3 (range, 8–14) achenes, 3.8 ± 0.4 (range, 1–12) of which 36% were destroyed by one or two larvae per head.

Novak and Foote (1968) reported that each larvae of *P. albiceps* destroyed three to six achenes as first and second instars. Infestation rates in *Aster puniceous* L. heads ranged from 7 to 79%, in heads of *A. praecaltus* Poiret from 6 to 42%, in *A. laevis* L. from 20 to 30%, in *A. novae-angeliae* L. from 15 to 25%, and in *A. pilosus* Willdenow <5%. Similarly, from 5 to 80% of the achenes in these infested heads were damaged by *P. albiceps*. Frick (1964) reported that 4.4% of the heads of *E. staechidifolium* Lagasca y Segura and 3.3% of the heads of tansy ragwort from one location in northern California were infested by *P. genalis* larvae, each of which damaged an average of 15.4 (range, 9–30) achenes. Seven and 5.7%, respectively, of tansy ragwort heads sampled during succeeding years contained *P. genalis* larvae that respectively destroyed averages of 1.5% of 1.3% of the achenes per head. Our data and Frick's (1964) data on *P. genalis* agree with the finding of Novak and Foote (1968) that even the most heavily infested hosts of *P. albiceps* managed to mature a "goodly number" of achenes.

Puparium.—The third instars of *P. genalis* pupariated within their feeding cells usually excavated off-center in heads of *E. lanatum* and loosely surrounded by fragments of achenes (Fig. 6F). The caudal ends of most puparia were directed towards the base of the flower heads and commonly rested within a feeding cavity in the convex receptacles. Some puparia in these heads were buried nearly their full lengths in the receptacles; whereas, a few others were formed above the unscarred receptacles among the achene fragments, pappus hairs, and damaged corollas. Receptacles were scored in 43 of 100 infested heads of *S. mohavensis* containing fully-grown third instars and puparia. In *Crepis acuminata*, each puparium was located within an individual, full-size achene where the larva had largely confined its feeding. In *C. occidentalis*, each puparium also was enclosed within an individual excavated achene, but early instars had fed on adjacent achenes. The receptacles were unscarred in infested flower heads of both *Crepis* spp., in which the third instars' solid diet apparently was supplemented by sap conducted through the caruncle to the surface of the feeding scar in the basal fragment of the excavated achene, as reported for *Procecidochares flavipes* Aldrich by Goeden et al. (1994).

Adult.—Wing displays.—Both sexes exhibited synchronous and asynchronous supination as described for *Aciurina thoracica* Curran (Headrick and Goeden 1993) and *Tephritis arizonaensis* (Goeden et al. 1993) and hamation as described for *Trupanea californica* (Headrick and Goeden 1991). The most common wing display in *P. genalis* was "lofting" with abdominal flexures, described here for the first time. Lofting consisted of supinating the wings and raising them above the body along a line closely parallel with the long axis of the body (Fig. 7). A feature of wing lofting in *P. genalis* was the concomitant abdominal flexures. The abdominal flexures mirrored the same rate and degree of loft as the wings. The halteres also were simultaneously depressed when the wings and abdomen were raised. Both sexes exhibited spontaneous lofting at other individuals, or at moving objects, but lofting was always a part of male courtship displays. Single males exhibited an agitation display of synchronous wing supinations.

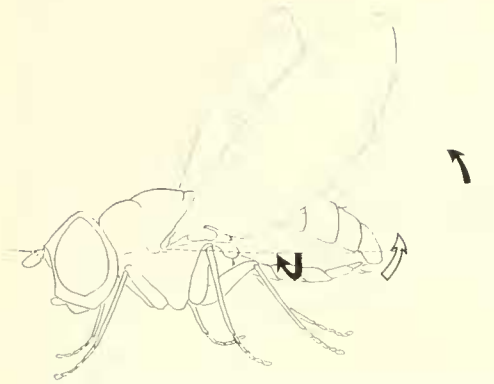

Fig. 7. Diagram of wing lofting by *P. genalis*. Solid arrows indicate movements of the wing blade. Open arrow indicates the movement of the abdomen during lofting.

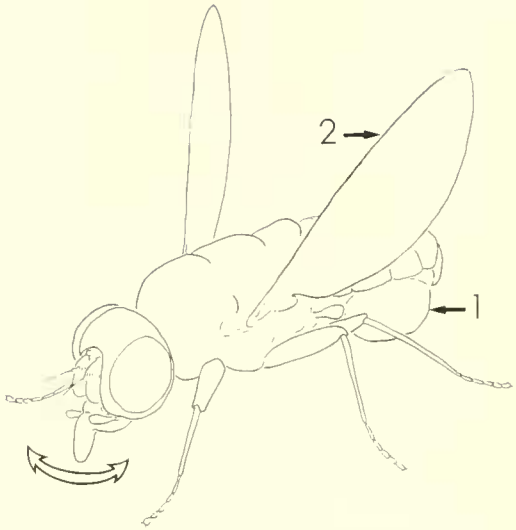

Fig. 8. Diagram of male courtship display and labellar wagging by *P. genalis*. 1—Abdominal pleural distension, 2—wing lofting; open double-headed arrow indicates the motion of the labellum.

The wings were extended from a resting position to 45° away from the midline of the body and held; then they were slightly supinated and vibrated synchronously 3–5 times per s. Wing vibration was 5–10° in the plane of the blade while each wing was extended and returned rapidly without further rotation. After three to five extensions, the wings were relaxed to ca. 20° from the midline of the body and then extended again.

Courtship.—Males displayed aggregation behaviors in proximity to females in the mornings in laboratory arenas. Their behaviors included abdominal pleural distension and wing lofting (Fig. 8-1, 2). Five male-female courtship interactions were observed from their inception to successful copulation. Males initially approached females in all five interactions; in three of these, males moved away from and re-approached females from one to three times. A female moved away from and re-approached a male twice in one of the five courtship interactions. When males approached females for courtship, they continued displaying wing lofting and abdominal pleural distension, and also front-leg waving and labellar wagging, a previously unreported behavior described here for the first time. Males extended their geniculate mouthparts while displaying to females at 2–50 mm distances. The labellum hung downward at ca. 90° from the rostrum (Fig. 8). The entire mouthpart structure was moved from side-to-side through ca. 120° at a rate of ca. 2 wags per s (Fig. 8). Episodes of front-leg waving and labellar wagging continued intermittently while males faced females, but ceased when a female turned away. Females did not extend their mouthparts toward males in response. Courtship displays by males in laboratory arenas led to mounting attempts; however, in field observations such courtship displays were not observed (see "Field observations," below).

Females responded to displaying males by staying (n = 4) or walking away (n = 7). Males attempted to mount females after courtship displays (n = 3), or males mounted females without prior displays (n = 3). This latter behavior was most commonly observed at the field study site (see below). A receptive female exhibited an acceptance display at a courting male by lowering her anterior end in a crouch (n = 3). The male then lowered his wings, deflated his pleura, and retracted his mouthparts as he mounted

the female from the front, then turned 180° and grasped her abdomen with his legs. Males were situated relatively forward on the female, with the head above the middle of the thorax of the female or just behind her head. The front legs of the male grasped the post pronotal lobes of the female, his middle legs wrapped around her abdomen near her thorax and his hind legs grasped the base of her oviscape. Males also mounted females without courtship displays and from any direction, and once mounted, they turned and grasped the female in a similar manner. Once a male mounted a female, he began copulatory induction behavior (CIB).

Copulatory induction behavior.—CIB was observed in the laboratory at its inception, or shortly after it began, with an additional four pairs of flies, and during field observations. Males used their middle and hind legs to simultaneously spread the wings of the female and to raise her abdomen and ovipositor from ca. 45° to 90° above the rest of her abdomen; thus, the ovipositor projected upward between the wings of the female (Fig. 6G). After the female was mounted and the apex of her ovipositor was lifted to the epandrium, CIB began. Mounted females remained passive or raised their front legs high above their heads in apparent attempts to grasp the head or front legs of the male (n = 3); however, the female's front legs were unable to reach the male. During CIB, *P. genalis* males pressed their hind tibiae and tarsi against the sides of the oviscape and rubbed asychronously dorsoventrally because of the 90° angle of the ovipositor relative to the abdomen. CIB was rapid, 5–6 strokes per s in short bursts of 2–3 s. Sustained CIB for 10–20 s occurred when females were unreceptive and did not exsert their aculeus, or when they exserted their aculeus against the males during copulation (see below). Receptive females exserted their aculeus usually within 2 min after CIB was initiated (n = 9). Unreceptive females did not exsert their aculeus and one male continued CIB for up to an hour before dismounting.

Copulation.—Mounted males continued with CIB after the aculeus was exserted and engaged by the male terminalia. When the aculeus was fully exserted, the body of the male was lifted away from the body of the female. In this position, the aedeagus was inserted into the gonopore and the aculeus slowly retracted. In the final copulatory position, the ovipositor was bent upward to ca. 80° with respect to the substrate and the rest of the abdomen (Fig. 6G). The male pressed his hind legs against the sides of the raised ovipositor throughout copulation. The wings of the female were spread ca. 45° away from the midline of the body and the male's wings were slightly parted.

The following activities were observed during all copulations. Both sexes formed feeding droplets (see "Droplet formation" below) and groomed. Females oriented and displayed asynchronous supinations toward moving objects. If agitated, a female exerted pressure on her aculeus. The male responded with CIB, or as observed on two occasions, by removing his fore tarsi from the female's thorax and stroking the vertex of her head. The female responded to the male touching her head by raising her front legs in an apparent attempt to dislodge the male's fore tarsi. The male then responded in turn by moving his fore tarsi to their normal copulatory position on the post pronotal lobe of her thorax. If agitated while in copula, a male displayed synchronous wing extensions with vibrations. This wing display continued until the stimulus was gone, then the male returned his wings to their resting position, overlapped atop his dorsum.

Copulations averaged 4.0 ± 0.10 h (range 1–9.5, n = 19) and were observed during daylight hours. However, five copulations began at 19:00 h PST or later and two began at 10:30 h PST and continued without artificial light after 24:00 h. Copulation ended with the male turning 180° and walking off

the dorsum of the female and pulling the aedeagus free as they moved apart (n = 5) (Fig. 6H).

Courtship for *P. albiceps* (Novak and Foote 1968) involved individuals of opposite sex facing each other at close range and raising their front legs to make "tarsal contact" with the other's head and antennae. This behavior most likely approximated the front-leg waving observed with males of *P. genalis* in the present study. Novak and Foote (1968) also reported that males and females approached each other, moved away, and re-approached several times after tarsal contact, which was consistent with our laboratory observations. However, *P. albiceps* adults were only observed to exhibit asynchronous supination, not lofting (Novak and Foote 1968). This is a biologically significant deviation in mating behavior from *P. genalis* and other species of *Paroxyna* (Headrick and Goeden, unpublished data).

Reproductive behaviors were not observed in the laboratory for *P. albiceps* by Novak and Foote (1968). *Paroxyna albiceps* emerged throughout the summer from its *Aster* hosts and remained closely associated with its host plants after emergence. Adults were not observed mating until late summer, after a rather extensive pre-mating/oviposition period (ca. 60 d) during which females remained reproductively immature (Novak and Foote 1968).

Droplet formation.—Adults formed droplets during their other activities and this feeding behavior was commonly observed in the afternoons. Droplets were ca. ⅓ the size of the head and clear. The geniculate mouthparts did not pump until the droplet reached full size. Males constricted their abdomens before and during droplet formation. Both sexes produced and imbibed ca. two droplets per min while feeding.

Field observations.—Distribution and abundance.—Plant crowns at the study site were measured along their maximum N/S and E/W axes and ranged from 4 × 7 to 18 × 27 cm (n = 16). Numbers of adults varied from 1 to 9 per plant and generally larger plants hosted more flies than smaller ones. Adults were active and perched on preblossom plants by 09:30 h. Both sexes rested on leaves, peduncles and flower heads, and exhibited wing lofting and abdominal flexures as observed in laboratory arenas. Adults visually oriented to moving objects. Males moved frequently from plant to plant and were easily disturbed. Females moved less frequently than males among plants, but actively explored many flower heads on individual plants for oviposition.

Male-Female interactions.—The first mated pair was observed at 09:45 h on a leaf in the sun. Their copulatory position was the same as described from laboratory pairings, i.e. the female's ovipositor was raised 45° to 90° relative to the rest of her abdomen and the male's head was positioned above the thorax of the female. The male of this pair displayed CIB during copulation as described from laboratory pairings.

Single males visually tracked individuals of both sexes and attempted to mount either males or females, jumping at them from up to ca. 5 cm. Male courtship displays were not observed in the field as had been recorded in laboratory arenas. Instead, males tracked individuals as they moved about on one host plant and from one plant to another. Males also moved toward ovipositing females and jumped at them in attempting mounting. Only two successful mountings of females were observed. However, males successfully mounted other males more often because males remained passive, and were not startled by nor jumped away from other males trying to mount them. A male that mounted another male positioned himself as he would on a female. He used his middle legs to spread the mounted male's wings and his hind legs to raise the mounted male's abdomen. The top male then began

CIB, placing his epandrium at the apex of the mounted male's abdomen, as the mounted male remained completely passive. One such mounted male raised his front legs upward, attempted to grasp the head of the male, like some mounted females. All males mounted on other males dismounted within a few seconds of initiating CIB and moved away. Fighting between males was not exhibited, thus a male's ability to discriminate between conspecific sexes was poor compared with other tephritid species observed in field studies (Headrick and Goeden 1990, unpublished data).

After unsuccessful mounting attempts of females engaged in oviposition, males walked around the surface of a flower head in distinctive, repetitive "figure eight" movements. The purpose of this behavior was not discerned.

When a male successfully jumped onto the dorsum of a female, he immediately positioned himself, held onto the female with his middle legs around her wing bases, and his front legs on her thorax, and began CIB as described above. In both field observations of mating pairs, continued CIB resulted in the female voluntarily raising her ovipositor. In one instance, a male was unable to move his hind legs behind and grasp the ovipositor and the female immediately lowered it; but he continued CIB and she again raised her ovipositor. The male pressed his epandrium against the apex again and she exserted her aculeus and intromission was gained.

In another field observation two males mounted a single female, but neither was in copula with her. They both rubbed her abdomen and ovipositor with their hind legs as in CIB. They remained like this for 15 min, the top male stepped off and flew away. The remaining male moved into a copulatory position and continued CIB. The female then raised her ovipositor and the male bent his abdomen downward while lifting the female's abdomen upward with his hind legs. He pressed his epandrium against her oviscape apex and continued CIB. Intromission was not gained and the female lowered her ovipositor. He raised her oviscape apex to his epandrium several more times and she finally exserted her aculeus. They remained in copula on their host plant for ca. 10 min, then flew out of sight.

Oviposition.—Females displayed oviposition behavior after 10:00 h. They typically displayed wing lofting while exploring for oviposition sites on the sides of pre-blossom flower heads. A female bent her abdomen and ovipositor downward perpendicular to the side of the flower head and began to probe, attempting to work the tip of her oviscape between the involucre bracts. Females ceased wing lofting while probing. Females probed the outer surfaces of flower heads briefly several times before exserting their aculeus into and through the bracts, depositing an egg centrally in the head as described above (Fig. 61). Ovipositional episodes in the field lasted ca. 2 min.

Mate-guarding.—Four pairs were observed in laboratory trials to end copulation with the male remaining on the female. To do so, a male raised his abdomen upward away from the female while he pushed the abdomen of the female downward with his hind legs, thus pulling the aedeagus free from the aculeus. Males remained on top of the females, and in two cases, initiated CIB after ca. 1 h followed by another copulation. Mate-guarding behavior among the Tephritidae has only previously been reported for the rare and unusual Australian species, *Phytalmia* sp. nr. *megalotis* Gerstaecker (Moulds 1977). In one instance, a female *P. genalis* oviposited while the male remained on her dorsum. Previously inseminated, lone females also oviposited in field and laboratory studies. Mate-guarding has been suggested as one way a male may insure that his sperm will be used to fertilize a female's eggs. Remaining with the female as she oviposits and copulating between oviposition

episodes is a classic example of mate-guarding (Parker 1978, Thornhill and Alcock 1983).

Mate-guarding in insects falls into one of two apparent categories which together comprise male competition for females (Thornhill and Alcock 1983): (1) male adaptation of attributes that make detection of an encountered female by the finder's rivals less likely and (2) male adaptation of attributes that make it physically difficult for another male to take a female from her original discoverer. To prevent takeovers, male insects most commonly remain joined to the female using some part of their anatomy (Thornhill and Alcock 1983). The latter strategy appears to apply to *P. genalis* males, which, by riding females in the mating posture, presumably restrict other males from copulating. Thornhill and Alcock (1983) defined the selective consequence of mate-guarding as time lost for acquiring additional females, and the 4 h that *P. genalis* males remained with females on average was a significant investment in time. Mate-guarding may have developed in this species as one strategy for males to insure some reproductive success if encounters with females are infrequent due to low population numbers (Parker 1978, Thornhill and Alcock 1983, Headrick and Goeden, unpublished data). This mating strategy can be coupled with observations of males attempting to mount any conspecific on the host plant irrespective of sex. If frequency of encounters is low, it may be adaptive to try to mount and copulate with anything closely resembling a conspecific female, and if successful, to remain then with the female until oviposition has occurred. Successful matings for a male may also increase with experience gained from frequent mounting episodes and CIB episodes.

Seasonal history.—*Paroxyna genalis* is multivoltine in southern California, reproducing in the flower heads of a succession of species of Asteraceae nearly throughout the year. No evidence of larval or pupal diapause was found until recently, even from samples of flower heads collected above the winter snow line in the mountains of southern California. Adults emerged from heads in late-summer and fall; larvae did not exit for pupariation in the soil or litter, as reported by Novak and Foote (1968) for *P. albiceps*. Frick (1964) similarly reported fall emergence of adults from flower heads in coastal, northern California, and speculated that *P. genalis* was nondiapausing and multivoltine. However, recent samples of flower heads of *Senecio hydrophilus* Nuttall collected in northern California from a pasture at Little Walker Cowcamp along the Little Walker River at 2070 m and from Pimentel Meadows at 2210 m, Mono Co., Toiyabe Nat. Forest, on 18.viii.1993 have yielded many puparia of *P. genalis* formed outside of the heads on the floor of the rearing cages and only a few adults. This indicates that *P. genalis* may diapause and overwinter as puparia in the High Sierras and more northerly latitudes in California and elsewhere in the U.S. and Canada.

Natural enemies.—The principal natural enemies of immature *P. genalis* were the solitary, primary, larval-pupal, endoparasitic, chalcidoid Hymenoptera, *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae). Also reared in limited numbers from bulk samples of flower heads containing *P. genalis* and *Trupanea* spp. were the following Chalcidoidea known to be associated with other native florivorous Tephritidae (however, their trophic relations, if any, with *P. genalis* were not confirmed by rearings from parasitized individuals): *Chlorocytus* sp. (Pteromalidae), *Colotrechnus* sp. (Pteromalidae), *Diglyphus* sp. (Eulophidae), and *Mesopolobus* sp. (Pteromalidae).

Total parasitization by *Eurytoma* sp. and *Pteromalus* sp. of larvae and puparia dissected and reared from subsamples of mature heads ranged from 16% (n = 43) in *E.*

lanatum, to 38% (n = 21) in *C. acuminata*, to 40% (n = 35) in *C. occidentalis*.

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